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ASPECTS OF THE PELAGIC ECOLOGY AND BEHAVIOR OF THE BLACK-CAPPED PETREL (*PTERODROMA HASITATA*)

J. CHRISTOPHER HANEY¹

ABSTRACT.—Recent seabird surveys off the coast of the southeastern United States indicate that petrel distribution is most influenced by the Gulf Stream and other warm water masses between 10° and 40°N latitude. Gulf Stream meandering and topographically induced current deflection affected petrel distribution at meso-scales (100–1000 km) between Florida and North Carolina. Locally (10–100 km), petrel distribution was influenced by the presence of upwelling associated with Gulf Stream eddies and the mesas, ridges, and hills on the Blake Plateau. Sea surface temperature and depth alone did not adequately characterize the petrel's marine habitat.

Petrels used three modes of flight, and their flight behavior was strongly influenced by wind speed. During the day they were most active in early morning and late afternoon, when all observed feeding took place. Petrels also may have fed crepuscularly and at night. Most feeding occurred in mixed species flocks at either natural food sources (fish and invertebrate swarms) or on chum at fishing vessels. Petrels did not rely exclusively on olfaction for locating food sources. They fed on cephalopods, small fish, and fauna associated with the macro-alga *Sargassum*. *Received 7 Jan. 1986, accepted 14 Apr. 1986.*

The Black-capped Petrel (*Pterodroma hasitata*), once thought to be extinct (Bent 1922), is the only gadfly petrel known to breed in the West Indies. The species has been observed infrequently during the last century. Only since the 1970s (Lee 1977, Lee and Booth 1979) have Black-capped Petrels been considered regular visitors to some offshore zones of the southeastern United States, apparently the species' primary nonbreeding range (Clapp et al. 1982). The sizes, locations, and chronologies of petrel breeding colonies remain little known (Wingate 1964, van Halewijn and Norton 1984). The Gulf Stream current is thought to be a principal factor

¹ Dept. Zoology, Univ. Georgia, Athens, Georgia 30602. (Present address: Alaska Fish and Wildlife Research Center, U.S.F. & W.S., 1011 E. Tudor Rd., Anchorage, Alaska 99503.)

influencing the marine distribution of this species (Clapp et al. 1982, Lee 1984). Here I examine the pelagic ecology and behavior of petrels observed off the coast of the southeastern United States in relation to Gulf Stream variation. Additional observations of postbreeding phenology, behavior, interspecific feeding associations, and foraging are also given for the species.

STUDY AREA AND METHODS

Observations of Black-capped Petrels were made during 173 days of seabird surveys in the western North Atlantic Ocean from 1982 to 1985. Except for a 14-day cruise from Boothbay Harbor, Maine, to Bermuda and return, all observations were made between 28° and 35°N latitude off the coast of the southeastern United States. The principal differences between the marine environment of this region and other western North Atlantic sectors stem from (1) the proximity of the Gulf Stream to shelf water masses; (2) a wide (80–160 km) and shallow continental shelf uninterrupted by ledges, banks, or submarine canyons; and (3) the absence of a typical continental slope (Atkinson et al. 1983). The Blake Plateau, a topographic anomaly that lies between the continental shelf and slope, extends 100–150 km seaward of the continental shelf before steep bathymetric gradients are encountered. Waters deeper than 1000–2000 m are not found within 150–250 km of the coastline in the study area (southern North Carolina to northern Florida).

My methods for counting seabirds have been described elsewhere (Haney and McGillivray 1985). Counts employed a 300-m band transect and 15-min count interval. This method permitted expressing the abundances of Black-capped Petrels either per surface area censused or per count hour (Table 1).

During 2326 counts I recorded date, latitude and longitude, heading of ship and birds, ship speed, time of day, visibility, sea height, wind speed and direction, depth, and sea surface temperature (SST). Foraging associations and behavior of Black-capped Petrels were recorded while conducting in-transect counts and when ships were on station.

The distribution and abundances of Black-capped Petrels were compared to long-term Gulf Stream current statistics (Olson et al. 1983), or to Gulf Stream System Flow Charts (National Oceanic and Atmospheric Administration, Miami, Florida) that gave synchronous daily summaries of oceanographic conditions within the study area and along the cruise track. Black-capped Petrels were counted and their abundances compared among seven Gulf Stream eddies that differed in age and size. The ages of eddies were determined by examining time series of Gulf Stream System Flow Charts for initial eddy formation. Age approximated elapsed time since onset of upwelling at the eddy. Eddy sizes were computed by measuring their areal coverage or surface area from the charts.

Black-capped Petrels exhibit considerable variation in size, color, and the extent of white on the nape and base of the tail (Harrison 1983, Lee 1984). All white-naped and white-rumped *Pterodroma* were treated as ecologically equivalent in this study. These morphs, however, may represent breeding populations that differ in dispersal, distribution, and breeding chronologies.

DISTRIBUTION AND PHENOLOGY

Black-capped Petrels are confined to tropical and subtropical water masses in the western North Atlantic Ocean between 10° and 40°N latitude (Fig. 1). The species is known to breed only on Hispaniola (Massif de La Selle and Massif de La Hotte in Haiti; Sierra Baoruco in the Dominican

TABLE 1
SUMMARY OF SHIPBOARD COUNT EFFORT OFF THE SOUTHEASTERN UNITED STATES
(1982–1985)

	Census hours	Surface area (km ²)
Inner shelf	91 (17) ^a	457.5 (18) ^c
Middle shelf	137 (26)	661.5 (27)
Outer shelf	158.5 (30)	669.0 (27)
Gulf Stream	143 (27)	668.4 (28)
Winter	58 (12) ^b	293.6 (12)
Spring	166 (31)	823.2 (33)
Summer	166 (31)	678.8 (27)
Fall	139.5 (26)	680.8 (28)
Total	529.5	2476.4

^a Inner shelf: 0–20 m depths; middle shelf: 21–40 m; outer shelf: 41–200 m; Gulf Stream: 201–900 m (% of census time by location).

^b Winter: Dec.–Feb.; spring: Mar.–May; summer: June–Aug.; fall: Sept.–Nov. (% of census time by season).

^c Surface area (% surface area by location or season).

Republic) and in the Sierra Maestra in Cuba (van Halewijn and Norton 1984; R. van Halewijn, pers. comm.).

At sea, almost all Black-capped Petrels have been seen near breeding colonies or along the Gulf Stream in the South Atlantic Bight (Cape Canaveral, Florida, to North Carolina) (Lee 1977, 1984; Clapp et al. 1982; Haney 1983). Petrels occur in winter and spring north and south of Hispaniola, and near Puerto Rico and the Virgin Islands (Morzer Bruijns 1967a; Norton 1983, 1984). There are also records from the central eastern Caribbean and near the leeward Netherlands Antilles, but apparently no reliable observations from the western North Atlantic Ocean east of the West Indies (Voous 1983; R. van Halewijn, pers. comm.), and no pelagic observations from the Gulf of Mexico (Clapp et al. 1982). An old record of the Black-capped Petrel off Brazil (AOU 1983) is apparently unsubstantiated by details (R. van Halewijn, pers. comm.).

Black-capped Petrels occur at least occasionally north or east of the South Atlantic Bight. Single birds and small groups have been seen off Virginia and Maryland (Rowlett 1977, Harrison 1983) and north to about 40°–45° in the northwest Atlantic off New England and southern Canada (Brown 1973; Lambert 1977, pers. obs.), areas that are directly or indirectly influenced by the Gulf Stream (Fig. 1). Black-capped Petrels may also occur east of the Gulf Stream in the western Sargasso Sea (Nieboer 1966, Morzer Bruijns 1967b), but I saw none during 2 weeks of daily observations in the Sargasso Sea in August 1984. The species is accidental in the northeast Atlantic. A single specimen record (1852) exists for En-

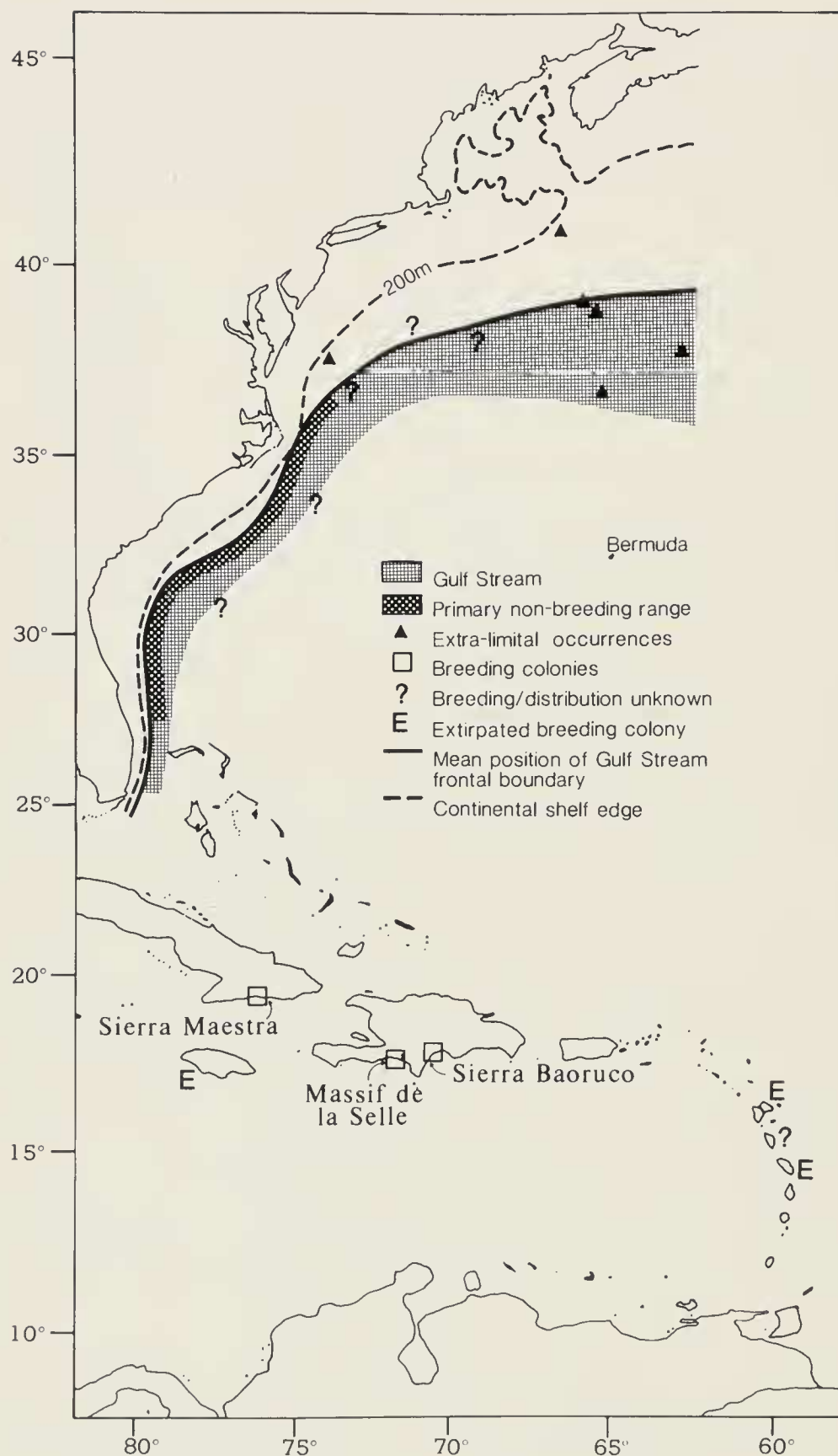


FIG. 1. Breeding colonies and marine distribution of Black-capped Petrels in the western North Atlantic Ocean. Extralimital occurrences north of 36° came from personal observations and literature accounts (Brown 1973, Lambert 1977, Rowlett 1977, 1980).

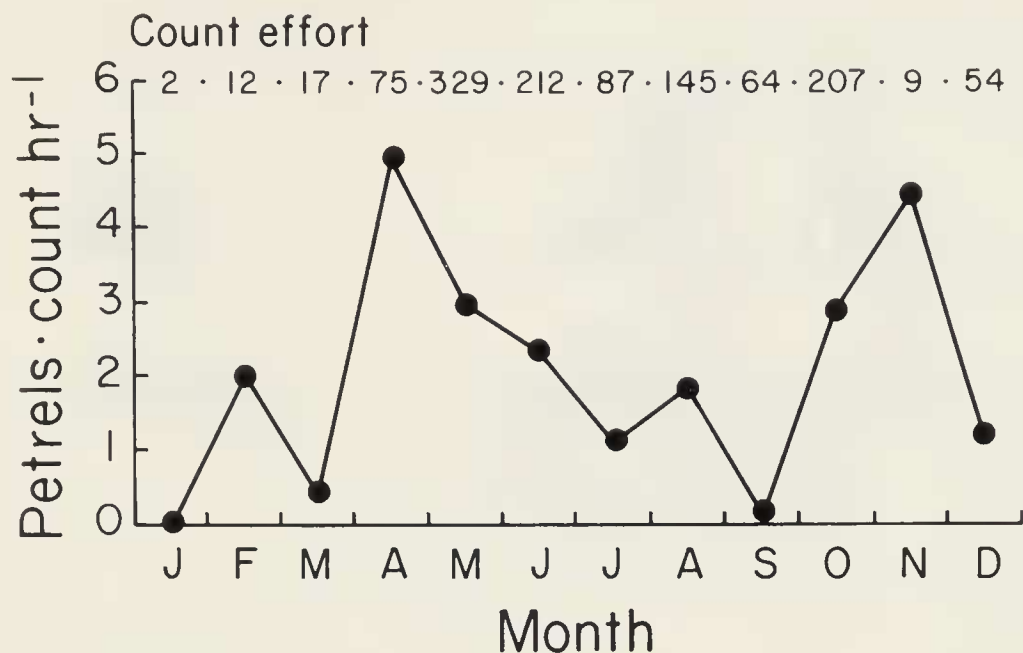


FIG. 2. Seasonal abundance of the Black-capped Petrel off the southeastern United States between 28° and 35°N latitude. Effort refers to number of 15-min counts made during the month on the outer shelf and in the Gulf Stream (Table 1).

gland, and there is a recent sight record from the Rockall Bank (Cramp and Simmons 1977, Bourne 1983).

Black-capped Petrels were observed offshore of South Carolina, Georgia, or Florida each month except January, when, because of inclement weather, very few offshore counts were conducted (Fig. 2). Peak abundances were recorded in spring and fall when the species moves from or to breeding colonies.

MARINE HABITAT

The primary marine habitat of the Black-capped Petrel off North Carolina lies seaward of the continental shelf break (200 m isobath), an area including, but not limited to, the Gulf Stream (Lee 1984). Petrels occurred almost exclusively within the cross-shelf interval of Gulf Stream frontal meandering in the South Atlantic Bight (Fig. 3). Gulf Stream position relative to the shelf changes during 2- to 14-day periods as a consequence of wave-like propagations along the current boundary (Lee and Brooks 1979, Lee et al. 1981, Lee and Atkinson 1983, Olson et al. 1983). Petrel affinities for the Gulf Stream current boundary resulted in changes in the species' distribution with respect to depth and distance offshore. Off Florida, Black-capped Petrels occurred over shallower depths and closer to land than farther north off Georgia and South Carolina. Broader cross-shelf distributions of Black-capped Petrels at higher latitudes also cor-

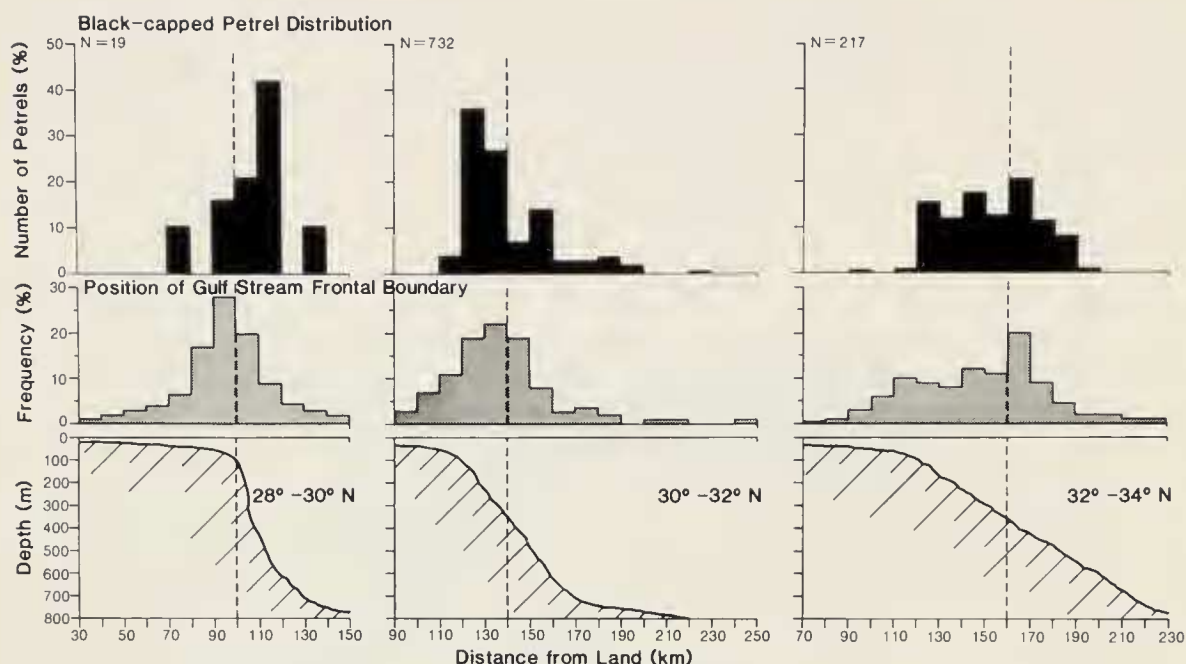


FIG. 3. Cross-shelf distribution of the Black-capped Petrel and its relationship to depth, distance from land, and the position of the western Gulf Stream frontal boundary at three intervals of latitude off the southeastern United States. Black-capped Petrel abundances were converted to frequency histograms (10 km interval) of the cross-shelf locations of individual birds (N refers to sample size). The frequency histograms of Gulf Stream frontal position are based on long-term satellite observations (Olson et al. 1983). The vertical dashed lines indicate mean frontal position.

responded to this increase in the cross-shelf range of frontal meandering (Fig. 3).

East of the western Gulf Stream frontal boundary, Black-capped Petrels were observed only over seamounts, submarine ridges, and mesas on the Blake Plateau. Small numbers of the petrels were seen feeding over and downstream of the Stetson Mesa ($30^{\circ}30'N$, $79^{\circ}30'W$) and Hoyt Hills ($32^{\circ}00'N$, $78^{\circ}30'W$). Petrels at these locations were primarily observed in or near internal wave crests resulting from topographic turbulence created by the current over steep undersea ridges and peaks.

One hundred to 1000-km scale changes in petrel abundance were correlated with increases in the amplitude of Gulf Stream meandering at higher latitudes (Fig. 4). Unstable meanders induce upwelling (Lee et al. 1981) and cause local increases in the biomasses of marine organisms in the South Atlantic Bight (Yoder et al. 1981, Atkinson and Targett 1983, Paffenhofer et al. 1984, Deibel 1985). Significantly, Black-capped Petrels were most abundant off northern Georgia and southern South Carolina (Fig. 4) where upwelling is most frequent, persistent, and extensive (Brooks and Bane 1978, Legeckis 1979, Bane 1983). Food biomasses may also be higher in this region because of downstream transport and accumulation

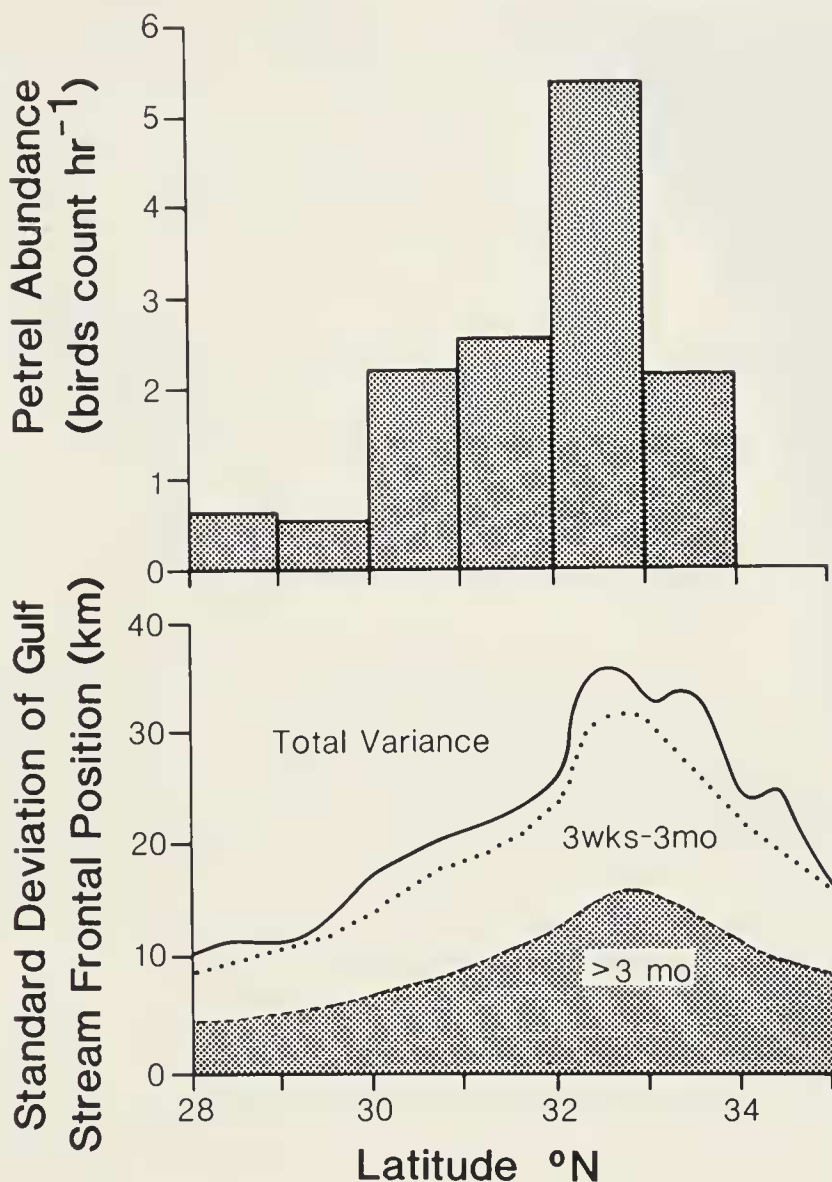


FIG. 4. Relative abundances of Black-capped Petrels at different latitudes off the southeastern United States. Changes in amplitude of Gulf Stream meandering are also shown as a function of latitude (Olson et al. 1983). A breakdown of meander variation at different time scales is included.

of marine organisms from upstream upwelling sites (cf. Yoder et al. 1981, Haney 1986a).

At shorter time scales (days) and at smaller spatial scales (10–100 km), Black-capped Petrels were unequally distributed along the Gulf Stream frontal boundary. Peak abundances occurred at temporary and kinetic frontal eddies (Fig. 5), upwelling features with elevated productivity (Yoder et al. 1981). Petrels were more abundant in the immediate frontal region at eddies (e.g., at the 28° and 29° isotherms) (Fig. 5), and in the resident Gulf Stream water itself (Haney 1986b). A few Black-capped

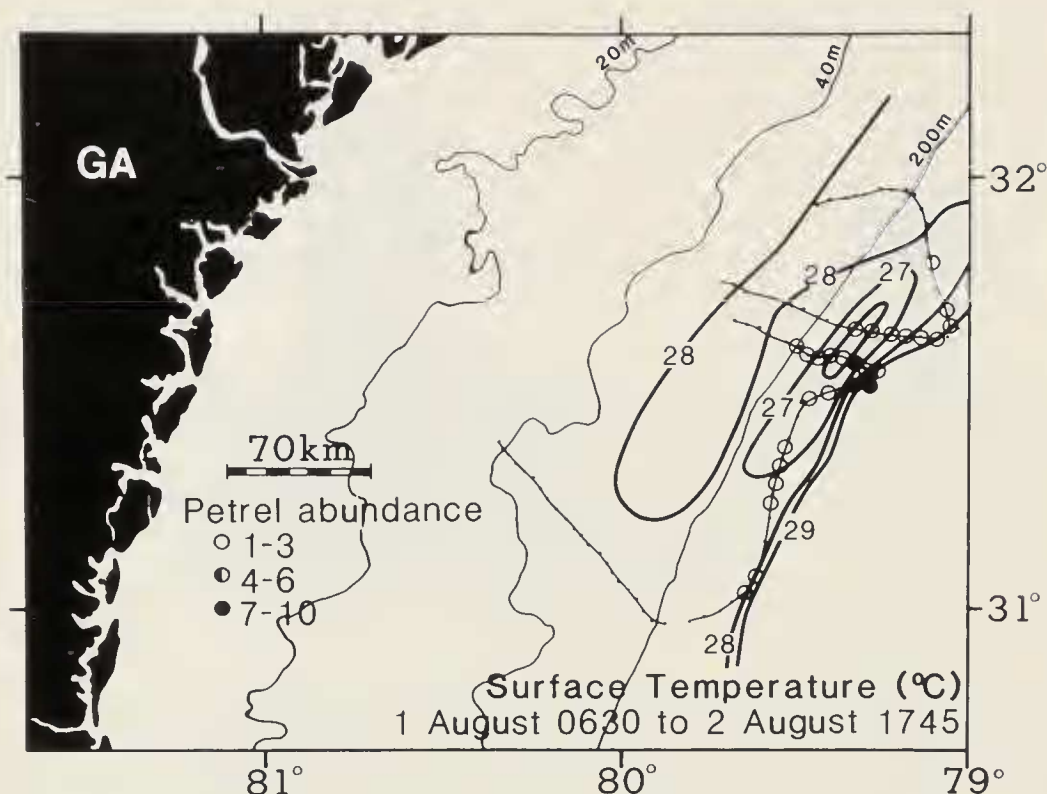


FIG. 5. Distribution and abundance of Black-capped Petrels at a Gulf Stream frontal eddy off the Georgia coast. Gulf Stream waters are those enclosed by the 28° isotherm. Cooler upwelled waters (25–28°C) are surrounded on three sides by warm filament and resident Gulf Stream water. Shelf waters are east of the 28° isotherm and 200-m isobath. Dotted line indicates ship cruise track during daylight hours.

Petrels, however, were occasionally observed in the adjacent upwelled eddy cold-core between the Gulf Stream and shelf waters (see also Lee 1984).

Peak petrel abundances occurred in the older and smaller eddies although no statistically significant correlations (r_s) were detected ($P > 0.10$). As upwelling intensity and the responses of marine organisms to upwelling vary among eddies (Yoder et al. 1983), petrels may have been differentially attracted to eddies that had different prey abundances or species composition, but the exact mechanisms and trophic pathways for the attraction are unknown.

SST and depth did not characterize the Black-capped Petrel's marine habitat over large geographic areas and long time spans. In the South Atlantic Bight, petrels were always observed in the relatively warmer offshore waters at or near the Gulf Stream; however, the absolute sea surface temperatures where petrels were observed varied extensively (20.5°–29.0°C), in part because of seasonal and latitudinal changes in the Gulf Stream (Atkinson et al. 1983). Conversely, Black-capped Petrels did not

occur during summer in shelf waters where SSTs may equal or exceed those in the Gulf Stream (Atkinson et al. 1983, pers. obs.). The influence of depth or bathymetry on petrel distribution was indirect, and was primarily exerted through steering effects of bottom topography on the position of the western frontal boundary of the Gulf Stream (cf. Brooks and Bane 1978, Legeckis 1979, Bane 1983) (Figs. 3, 4).

BEHAVIOR

Petrels usually flew in rapid "roller coaster" flight on bowed and angled wings that produced a distinctive bounding or rising and falling progression (Harrison 1983). Occasionally, they rose to 20–25 m above the sea at the peaks of the arcs. The extent of wing-flapping in this flight mode was inversely related to wind speed. At wind speeds \leq about 6 knots, petrels used a very slow and labored flight with many deep, rapid wingbeats, particularly when taking off from the ocean surface. Gull-like soaring on horizontal wings from 50–100 m above the ocean surface was observed rarely during moderate wind conditions (6–15 knots).

In higher winds Black-capped Petrels may sometimes spring directly into the air from the water surface (Harrison 1983). In low winds (≤ 6 knots), they run along the ocean surface for 2–4 m before taking flight (Haney 1983:fig. 2).

Relative petrel abundances increased from Beaufort force 2 to a peak at force 5 (17–21 knots) (Fig. 6). Individuals were not observed in winds ≤ 4 knots, except when sitting birds were flushed from the ocean surface by ship passage. The majority (72%; $N = 19$) of all sitting birds observed during transits, as well as 100% ($N = 13$) of nonfeeding sitting petrels, were recorded at wind velocities ≤ 4 knots. Unless petrels are more difficult to detect under conditions of low wind velocity when sitting on the ocean surface, these data suggest that petrels are dependent upon higher wind velocities for foraging and dispersal.

Black-capped Petrels were active during all daylight hours (Fig. 7) with an apparent peak in activity from 07:00–09:00 h and a less pronounced peak from 17:00–19:00 h. Petrels were seen flying in the ship's high-beam search lights at night, although no feeding was observed during these limited observations. All 8 natural (Table 2) feeding aggregations occurred before 09:00 h or after 15:00 h. All 6 chum-feeding aggregations occurred after 15:00 h. *Pterodroma* petrels exploit diel vertically-migrating, mesopelagic nekton (Imber 1985), which selects for crepuscular or nocturnal feeding.

Although petrels were generally silent, individuals at chum slicks occasionally uttered a bleating or "croaking" note, *waaahh* or *aaa-aw*, when feeding (cf. Wingate 1964, Imber 1985).

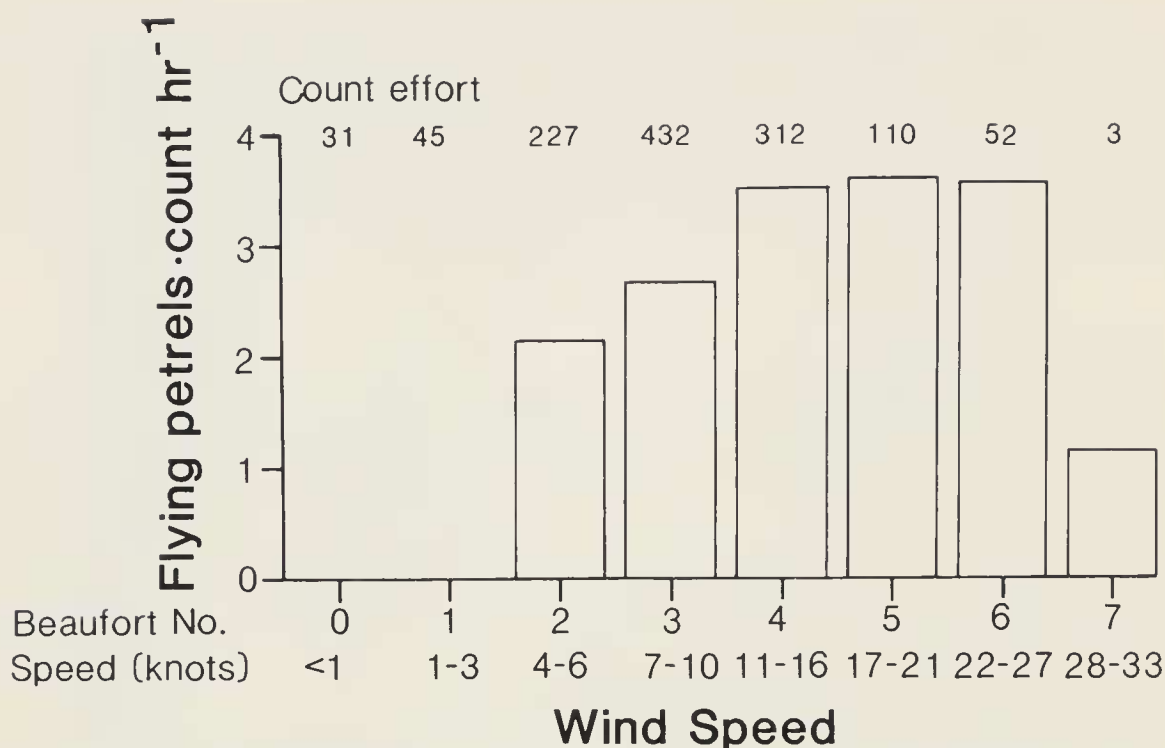


FIG. 6. Relative abundance of initially-flying (see text) Black-capped Petrels as a function of wind speed. Effort refers to the number of 15-min counts made at a particular interval of wind velocity on the outer shelf and in the Gulf Stream.

FORAGING AND FEEDING

The majority (96%) of petrel feeding bouts ($N = 25$) occurred in flocks, 88% of which included other species. Petrels fed with 12 other species ($\bar{x} = 4.3$ species/flock; range = 2–8) at baitfish or invertebrate swarms; most frequently with Cory's Shearwaters (*Calonectris diomedea*), Greater Shearwaters (*Puffinus gravis*), Audubon's Shearwaters (*P. lherminieri*), and Pomarine Jaegers (*Stercorarius pomarinus*) in summer, and with Herring Gulls (*Larus argentatus*) and Black-legged Kittiwakes (*Rissa tridactyla*) during winter. Petrels fed with 10 seabird species ($\bar{x} = 3.8$ species/flock; range = 3–6) at chum slicks, including Greater Shearwaters, Wilson's Storm-Petrels (*Oceanites oceanicus*), and Pomarine Jaegers in summer and Herring and Laughing gulls (*L. atricilla*) in winter. Other less common feeding associates included South Polar Skua (*Catharacta maccormicki*) and Common (*Sterna hirundo*), Bridled (*S. anaethetus*), and Sooty terns (*S. fuscata*). Both Parasitic (*Stercorarius parasiticus*) and Pomarine jaegers attempted to parasitize nonflying feeding petrels.

My observations of Black-capped Petrels feeding at chum are the first reports for this species (cf. Lee 1979, pers. comm.). During this study petrels frequently flew in to inspect fresh waste fish and fish and chicken entrails near fishing boats. Petrels settled on the water and consumed the

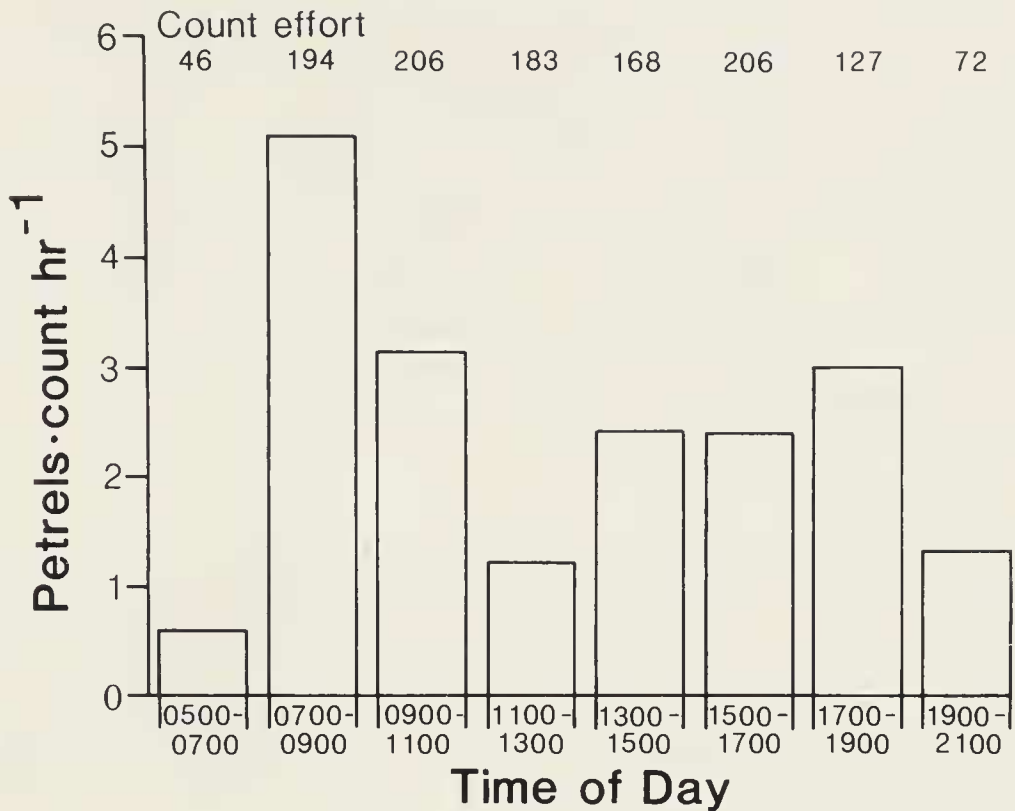


FIG. 7. Diel activity patterns of Black-capped Petrels. The numbers of flying birds per time interval are illustrated. Effort refers to the number of 15-min counts made within a particular time interval on the outer shelf and in the Gulf Stream.

chum, occasionally flying off with large pieces, or attempting to steal the food items from other petrels. On 13 April 1984, 65 petrels fed on fish entrails, with 5 to 10 individuals on the ocean surface continuously. As with several other Procellariiformes (Guzman and Myres 1983), Black-capped Petrels may scavenge discarded waste only when natural foods are not abundant or reliable, such as when large numbers of migrating individuals are locally concentrated.

Black-capped Petrels do not rely exclusively on olfaction for locating food sources as do certain procellariiform birds that are selectively attracted to food-related odors from downwind (Hutchinson et al. 1984). Petrels frequently flew in to inspect seabird individuals or flocks exhibiting foraging behavior from upwind, or from all compass directions.

Petrels used at least 3 foraging postures when feeding: (1) sitting on the ocean surface with wings outstretched and sharply angled backward; (2) aerial dipping and pattering (Ashmole 1971), with their feet extended and touching the ocean surface but still remaining airborne; and (3) less commonly sitting on the ocean surface with folded wings and the head and neck submerged underwater. The latter appeared to be similar to the foraging behavior of the Audubon's Shearwater (Haney 1986c).

TABLE 2
PERCENTAGE OF BLACK-CAPPED PETRELS IN MIXED-SPECIES SEABIRD FEEDING FLOCKS

Food source	Number of petrels		% petrels	
	Mean \pm SD	Range (N)	Mean	Range
Natural ^a	5.8 \pm 4.4	1–12 (12)	27	1–92
Chum ^b	12.6 \pm 18.6	3–65 (10)	47	15–97
Total	8.9 \pm 13.1	1–65 (22)	36	1–97

^a Shoaling baitfish or unidentified invertebrate swarms.

^b Fish entrails, whole small fish, chicken entrails, and fat.

Petrels spent very little time on the ocean surface. On 5 May 1983, P. W. Stangel (pers. comm.) observed aerial “flushing” and chasing of flying fish by two Black-capped Petrels but did not observe successful capture. On one occasion a petrel was seen diving 3–4 m from the air to, but not beneath, the ocean surface at an angle of 45–60°. This behavior resembled “belly flop” diving or surface plunging by gulls (Ashmole 1971). Petrels were not seen diving beneath the ocean surface.

Petrels fed alone and with other seabird species over schools of baitfish driven to the ocean surface by large predatory fish (e.g., bonito, blue-fin tuna, and Spanish mackerel). They also fed near patches of *Sargassum* where seabird food items may be abundant (Haney 1986c).

Little information is available on the diet of Black-capped Petrels (Clapp et al. 1982). Stomach contents of 3 petrels collected off Georgia (UGAMNH 5243, 5344, 5351) included squid beaks, disarticulated fish bones, fish lenses, whole squid (\bar{x} length = 47.5 mm, range 25–70 mm, N = 4), and one planehead filefish (*Monocanthus hispidus*; length = 40 mm). Other gut contents included very small pieces of petroleum residue, small feathers, paper, and *Sargassum* algal blades. The presence of the algal plant material in all 3 specimens, apparently ingested incidently, and the consumption of *M. hispidus*, suggest that this species forages on *Sargassum*-associated fauna (see Haney 1986c).

DISCUSSION

The nonbreeding range of the Black-capped Petrel is centered in the South Atlantic Bight between North Carolina and Florida. Petrel records off Florida originate from the Cape Canaveral region northward (Clapp et al. 1982). It thus seems likely that Black-capped Petrels migrate from West Indies breeding colonies north and east of the Bahamas via the Antilles Current rather than through the Straits of Florida. The seasonal abundance patterns of petrels (Fig. 2) suggest that the species is widely

distributed during the midsummer near the Gulf Stream to 36°, and perhaps farther north to 40°–45°N. Pelagic surveys in the northwest Atlantic (Brown et al. 1975, Rowlett 1980, Powers 1983) have not been extensive on the continental slope and more oceanic marine habitats of this region. Petrels may occur regularly farther north than present records suggest, especially where Gulf Stream meanders and warm core rings occur near the shelf edge (Rowlett 1980; Haney, unpubl. data).

Black-capped Petrels present off the southeastern United States during the winter breeding season may not yet be reproductively mature, or they may be nonbreeding adults that fail to return to the West Indies. Breeding *Pterodroma* may range up to a few thousand kilometers from nesting sites (Warham et al. 1977), and Black-capped Petrels could disperse to the southeastern United States between incubation shifts (Clapp et al. 1982). Another possibility is that breeding cycles of Black-capped Petrel populations among or within islands are not synchronous such that part of the population breeds in winter while part of the population breeds at another time of the year.

Productivity in the surface waters of the Gulf Stream is very low (Yoder et al. 1983). Few seabirds occur in the Gulf Stream except near the current boundary and where current-generated turbulence at seamounts on the Blake Plateau creates upwelling. The Black-capped Petrel is the only seabird present in the Gulf Stream all year. The behavioral and structural adaptations of gadfly petrels have enabled effective exploitation of ocean niches where prey are widely dispersed (Imber 1985). Their low wing loadings allow efficient gliding (Warham 1977), but not sustained flapping flight. As a result, the Black-capped Petrel is dependent on wind (Fig. 7) for long-distance foraging and dispersal within this oligotrophic environment.

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COLOR PLATE

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